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Evolution of an invasive phenotype: shift to belowground dominance and enhanced competitive ability in the introduced range

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Abstract In response to novel selection pressures in an introduced range, non-native species may evolve more competitive phenotypes unique from those of their native range. We examined the existence of an invasive phenotype in the herbaceous perennial *Artemisia vulgaris*, a frequent invader of the Northeast and Mid-Atlantic US. Populations from both the native (European) and the introduced (North American) ranges were grown in intra-specific competition (same population), inter-specific competition with the native perennial herb *Solidago canadensis*, and alone in a common garden to quantify shifts in resource allocation and neighbor effects on performance and competitive ability. Without competition, introduced *A. vulgaris* populations were much shorter than native populations, but germinated earlier, produced more ramets, more belowground and total biomass, and maintained higher root-to-shoot ratios. Under inter- and intra-specific competitions, introduced *A. vulgaris* populations were shorter, but produced more ramets, belowground, and total biomass than native populations. *S. canadensis* belowground and total biomass were more highly suppressed by introduced than native *A. vulgaris*. Our data suggest that since the introduction to North America, *A. vulgaris* has evolved a more competitive invasive phenotype characterized by many short ramets with more extensive root/rhizome networks. This rapid evolutionary shift likely benefits *A. vulgaris* in its introduced range by allowing establishment and subsequent dominance in dense stands of existing vegetation.

Keywords *Artemisia vulgaris* · Common garden · Competition · Mugwort · Resource allocation · *Solidago canadensis*

Introduction

From climate change to the global mixing of species, research continues to document human impacts on the environment. Palumbi (2001) refers to humans as the "world's greatest evolutionary force," because we impose selection pressures (from increased atmospheric CO_2 to prodigious use of antibiotics) affecting nearly all taxa. In addition to our direct effect on evolutionary trends, humans also introduce organisms to novel environments, often vast distances from their native range. Many of these new environments present strong abiotic selection pressures to naïve genotypes (Caño et al. 2008; Vellend et al. 2007)—inhibiting germination or preventing establishment of arriving disseminules, resulting in

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very few successful introductions (Williamson and Fitter 1996). Propagules that do survive and reproduce are often genetically bottlenecked and highly susceptible to genetic drift—at least in the early stages of invasion or until subsequent, genetically variant, propagules arrive (Lockwood et al. 2005).

Alternatively, novel habitats may lack strong biotic selection pressures, due to the absence of the pathogens and specialist herbivores found in the native range (Colautti et al. 2004; Mitchell and Power 2003). This 'release' from natural enemies in the introduced habitat may select for phenotypes allocating relatively fewer resources toward now superfluous defense structures and chemistry (Blossey and Notzold 1995). The combination of reduced herbivory and disease and exposure to a novel environment can favor (select for) phenotypes that germinate earlier, produce more aboveground biomass, grow faster, and are more fecund (Blair and Wolfe 2004; Blossey and Notzold 1995; Brown and Eckert 2005; Grosholz and Ruiz 2003; Siemann and Rogers 2003). The net effect can be a rapid evolutionary shift to a phenotype unique to the introduced range with greater competitive ability compared with individuals in the native range (Blair and Wolfe 2004; Hairston et al. 2005; Lee 2002; Vellend et al. 2007). Therefore, it is of value to understand phenotypic shifts between geographic regions.

Few studies investigating the presence of an invasive phenotype have assessed the competitive abilities of native and introduced populations (Bossdorf et al. 2005 and references therein). Therefore, it is difficult to assess whether phenotypic differences in the introduced populations actually confer enhanced competitive ability. The few studies that have examined competitive ability have unfortunately only included a 'with' and 'without' competition comparison (Blumenthal and Hufbauer 2007; Blair and Wolfe 2004; Bossdorf et al. 2004; Vilà et al. 2003, except McKenney et al. 2007), which precludes elucidation of neighbor identity effects (Bossdorf et al. 2005). Including both inter- and intraspecific competition treatments as well as a competition-free control would more fully reveal competitive mechanisms and resource allocation patterns (Bazzaz et al. 1987).

One well-established method to determine phenotypic variation for ecological traits of interest is to grow native and introduced populations of the target species in a common garden (Hendry and Kinnison 1999). With adequate representation from both ranges, phenotypic divergence can be estimated efficiently, and if divergence in these characters is observed, then it presents evidence for genetic differentiation (Bossdorf et al. 2005). Most common garden studies have focused on aboveground biomass or seed production as fitness metrics (Bossdorf et al. 2005 and references therein). Aboveground biomass and seed production may be adequate metrics of fitness for annual plant species, but many invaders also reproduce vegetatively (Pyšek 1997), with clonal expansion largely responsible for local dispersal and competitor displacement (Barney et al. 2005). In addition, belowground competition for resources (e.g., water, nutrients) can often be more intense than competition for resources aboveground (i.e., light) due to similarities in belowground allometry (Casper and Jackson 1997). Root interactions between introduced plants and their native competitors remain largely unstudied, despite the importance of belowground interactions in influencing competitive outcomes (Wilson 1988). Therefore, quantification of aboveground and belowground dynamics between introduced and native populations, especially in response to a common competitor in the introduced range, would provide valuable insight regarding the mechanisms contributing to successful invasions.

The objectives of this study were to: (1) assess the variation among native and introduced populations of *Artemisia vulgaris* for specific phenotypic traits related to competitive ability; (2) compare phenotypic responses between native and introduced populations under various competitive environments; and (3) determine if an endemic 'invasive phenotype' exists in the introduced range that is distinct from the 'native phenotype.' We hypothesized that introduced populations would germinate earlier, grow taller, and would produce more above *and* belowground biomass when compared with native populations. Additionally, we postulated that introduced populations would be more competitive (i.e., inter-specific competition would be more asymmetric than intraspecific competition) than native populations.

Methods

Plant material and experimental design

The invasive perennial *A. vulgaris* L. (mugwort) was used as the model system to address the above objectives. *A. vulgaris* has a long history of human uses in its native Eurasian range (Barney and DiTommaso 2003), and has likely been introduced in many different locations and times in North America where it is non-native (Barney 2006). *A. vulgaris* is a vigorous competitor along roadsides and old fields, often displacing native vegetation along a distinct invasion front (T.H. Whitlow, personal observation). Viable seeds are produced annually, but vegetative reproduction and propagation is the principal mechanism for colonizing neighboring habitats (Barney et al. 2005). We selected the North American native perennial herb *Solidago canadensis* L. (*Solidago* hereafter), as the introduced-range competitor for this study, as both species are members of the Asteraceae, have similar life history traits and environmental tolerances, and occupy similar habitats (e.g., old fields).

A. vulgaris germplasm for this study was collected by the authors, collaborators, or purchased from sources with verifiable collection locations (Table 1), and stored dry at 4°C until use. In April 2006, seeds of 15 European (EU) and 12 North American (NA) populations of *A. vulgaris* (Table 1) and locally collected *Solidago* were sown in soil-less media. Flats were maintained in a greenhouse at 26/23°C day/night temperatures with natural lighting and watered as needed. The day of emergence was recorded for each seedling. Five weeks after seeding,

Table 1 Locations of European- and North American-collected *A. vulgaris* populations and number of replications per treatment used in this common garden study. Single *A. vulgaris* (A), two *A. vulgaris* (AA), and one *A. vulgaris* and one *Solidago* (AS) per pot treatments were used in addition to 20 replicates each of single (S) and double *Solidago* (SS)

Origin	Latitude, longitude		Replications per treatment		
			A	AA	AS
Europe	44.9°N, 20.3°W	Belgrade, Serbia	10	10	9
	45.6°N, 20.0°W	Bečej, Serbia	10	10	10
	52.5°N, 13.4°W	Berlin, Germany	3	0	3
	–	Germany	10	10	10
	48.0°N, 11.6°W	Munich, Germany	10	9	10
	49.4°N, 11.1°W	Nürnberg, Germany	10	10	10
	47.7°N, 8.1°W	Herrischried, Germany	10	10	10
	53.2°N, 9.2°W	Horstedt, Germany	10	10	10
	44.9°N, 5.8°W	Nantes, France	6	3	6
	48.9°N, 1.5°W	Saint-Gilles, France	10	11	10
	51.4°N, −0.8°W	Berkshire, England	3	0	3
	51.4°N, −0.8°W	Berkshire, England	10	10	10
	51.4°N, −0.8°W	Berkshire, England	2	0	2
	51.5°N, −0.2°W	London, England	2	0	2
	50.1°N, 14.4°W	Prague, Czech Republic	4	0	3
		Total	110	93	108
North America	46.7°N, −71.4°W	Québec, Canada	10	10	9
	42.4°N, −72.5°W	Amherst, Massachusetts	10	9	9
	40.3°N, −75.9°W	Shillington, Pennsylvania	6	7	8
	40.9°N, −79.9°W	Butler, Pennsylvania	7	3	8
	40.9°N, −73.1°W	Stony Brook, New York	10	9	8
	40.9°N, −73.1°W	Port Jefferson, New York	10	10	9
	40.9°N, −73.2°W	Oyster Bay, New York	10	10	9
	40.8°N, −73.7°W	Queens, New York	10	10	8
	42.5°N, −76.5°W	Ithaca, New York	8	7	7
	39.9°N, −75.2°W	Camden, New Jersey	10	9	8
	40.9°N, −74.2°W	Wayne, New Jersey	10	9	9
	33.2°N, −84.3°W	Griffin, Georgia	10	10	10
		Total	111	103	102

individual seedlings were transplanted in 15.3 cm top-diameter pots lined with weed fabric and filled with white sand (pH 6.5), and top-dressed with 6 g slow-release fertilizer Osmocote 14-14-14 (N–P-K). Individual plants were tagged so as to be able to track them through harvest. At the time of transplanting, the height (cm) of each shoot was recorded.

The competitive dynamics of *A. vulgaris* were examined using plants derived from populations from both the native (15 accessions, EU) and the introduced (12 accessions, NA) ranges. The following three treatments were imposed on all 27 accessions: single *A. vulgaris* (A), two *A. vulgaris* individuals of the same population (AA), one *A. vulgaris* and one *Solidago* (AS). *Solidago* treatments consisted of one (S) or two (SS) *Solidago* individuals, which were used to calculate competition indices for *Solidago* relative to *A. vulgaris*. The AA and AS treatments were used to determine neighbor identity effects (sensu Bossdorf et al. 2004). Pots were arranged in a completely randomized design in a 15 × 60 m^2 turfgrass field (*Festuca* spp.). Pots were placed into pre-drilled holes spaced 1 m apart in the field so the tops of the pots were level with the soil surface. Turfgrass was mown to a height of 2.5 cm as needed to prevent interaction with treatments. Overhead irrigation of ~2.5 cm was applied when needed—usually one to two times per week.

Data collection and statistical analyses

In order to avoid genetic mixing between resident *A. vulgaris* populations and those used in this study, target plants were destructively harvested before flowering. Eight weeks after transplanting (13 weeks after germination), the experiment was terminated, which coincided with inflorescence initiation. The following variables were recorded for each plant in each pot: height of tallest ramet and total number of ramets. Aboveground tissue for each plant was cut at soil level and dried at 70°C until constant mass was achieved, and then biomass determined by weighing. Pots were placed at 4°C until roots could be washed (<1 week). Belowground tissue was harvested by washing soil off roots/rhizomes with water. Roots of different plants were separated easily by pulling them apart manually. Belowground tissue was dried at 70°C until constant mass was achieved, and biomass determined by weighing. Root-to-shoot biomass ratios (R/S) were calculated for each individual.

In order to determine whether the measured-dependent variables differed between populations from the native range (EU) and the introduced range (NA), a mixed-model ANOVA was used. Population origin (EU and NA), competition treatment (A, AA, AS), and the interaction between origin and treatment were considered fixed effects, while population nested within origin was considered a random effect. Preplanned contrasts were performed between origins within competition treatments with a corrected error of $\alpha = 0.05/3(\text{contrasts}) = 0.017$ for each dependent variable. All analyses were performed using the JMP v5.1 statistical software package (Cary, NC). All means presented are least square means ± 1 SE.

Competition indices

We calculated plant competition indices for each *A. vulgaris* origin (EU and NA) among the various competition treatments. These indices allow comparisons of the competitive strength between native and introduced *A. vulgaris*, as well as their relative effects on *Solidago*. The relative competitive performance index (Cpi) quantifies the proportional decrease in plant fitness due to competition (Keddy et al. 1998), and was calculated as:

$$\mathrm{Cpi} = \left[\left(P_{\mathrm{single}} - P_{\mathrm{comp}}\right)/P_{\mathrm{single}}\right] \times 100,$$

where P_{single} is *A. vulgaris* performance when grown alone (A), and P_{comp} is *A. vulgaris* performance when grown in (intra- or inter-specific) competition (AA or AS). If $\mathrm{Cpi} = 0$, then *A. vulgaris* performance is unaffected by the presence of a neighbor (i.e., no competition). If $\mathrm{Cpi} > 0$, then *A. vulgaris* performance is greater without competition, and if $\mathrm{Cpi} < 0$ then *A. vulgaris* performance is greater with competition. To compare *A. vulgaris* fitness when grown in intra-specific competition (AA) to *A. vulgaris* grown in inter-specific competition with *Solidago* (AS) (i.e., does neighbor identity matter?), we calculated the relative competition index (RCI) (Jolliffe et al. 1984) as:

$$\mathrm{RCI} = [(P_{\mathrm{mono}} - P_{\mathrm{mix}})/P_{\mathrm{mono}}] \times 100,$$

where P_{mono} is *A. vulgaris* performance when grown in monoculture (AA), and P_{mix} is *A. vulgaris* performance when grown in mixture (AS). If $\mathrm{RCI} = 0$, then *A. vulgaris* performance does not differ based on neighbor identity (i.e., AA = AS). If $\mathrm{RCI} > 0$, then

A. vulgaris performance is greater when grown with an *A. vulgaris* neighbor, and if RCI < 0 then *A. vulgaris* performance is greater when grown in the presence of a *Solidago* neighbor. Cpi and RCI were calculated for each variable (height, total biomass, etc.) as the mean of individual plants within each population, followed by averaging populations across origin. Cpi and RCI values were also calculated for *Solidago*. Pairwise contrasts were made between origins for all competition indices except S–SS.

Results

Life history and allometric variables

Seedlings of introduced North American *A. vulgaris* populations emerged earlier than European populations ($\sim$4 days: $F_{1,25} = 18.5, P < 0.0001$). However, by the end of the study, native (EU) *A. vulgaris* was 27% taller than introduced (NA) *A. vulgaris* across all treatments, although they had 61% fewer ramets per clone, and 18% less total biomass (Table 2). Averaged across origins, *A. vulgaris* individuals in the AA treatment had 76, 52, and 65% less aboveground, belowground, and total biomass, respectively, than *A. vulgaris* individuals grown alone (A), while individuals in the AS treatment had 31, 28, and 30% less aboveground, belowground, and total biomass, respectively, than *A. vulgaris* individuals alone (A).

A significant origin by competition treatment interaction was found for height, number of ramets, aboveground and total biomass, and R/S ratio (Table 2). Introduced *A. vulgaris* was shorter, but yielded more ramets than native individuals in all competitive environments (Fig. 1a, b). Aboveground biomass was greater in introduced *A. vulgaris* without a neighbor or with a *Solidago* neighbor (Fig. 1c). Belowground and total biomass were always greater in introduced than native populations, regardless of competitive environment (Fig. 1d, e). R/S ratios were higher in introduced populations in intra-specific competition and without a neighbor (Fig. 1f).

Competition indices

Within a population origin, the relative Cpi was typically greater for intra-specific competition (A–AA) than for inter-specific competition (A–AS) (Table 3). Although we could not compare statistically, *Solidago* was more highly suppressed by an *A. vulgaris* neighbor, native, or introduced, than another *Solidago* (S–AS > S–SS). The RCI was larger (more negative) for introduced populations than for native populations in ramet number and aboveground biomass (Table 3). *Solidago* individuals maintained higher fitness (RCI nearer zero) with native *A. vulgaris* neighbors with respect to belowground biomass and R/S ratio (Table 3).

Discussion

Averaged across all competition treatments, introduced *A. vulgaris* seedlings emerged earlier, and produced more ramets and belowground and total biomass than native populations. However, introduced *A. vulgaris*

Table 2 Mixed-model *F*-statistic values and probabilities for independent variable effects on six measured dependent variables for *A. vulgaris*

Source	df	Height (cm)	Number of ramets	Aboveground biomass (g)	Belowground biomass (g)	Total biomass (g)	R/S ratio
Origin (O)	1	17.1***	11.4***	3.7	6.6*	9.6**	2.1
Population [Origin]	25	11.1***	10.7***	6.8***	6.3***	4.9***	12.0***
Treatment (T)	2	18.6***	14.4***	238.5***	54.6***	171.4***	10.2***
O × T	2	3.1*	3.9*	6.7**	1.4	3.9*	3.1*
Error	781						

Population nested within origin was treated as a random variable, while all other variables were fixed. Treatment refers to competitive environment: A, AA, or AS

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$

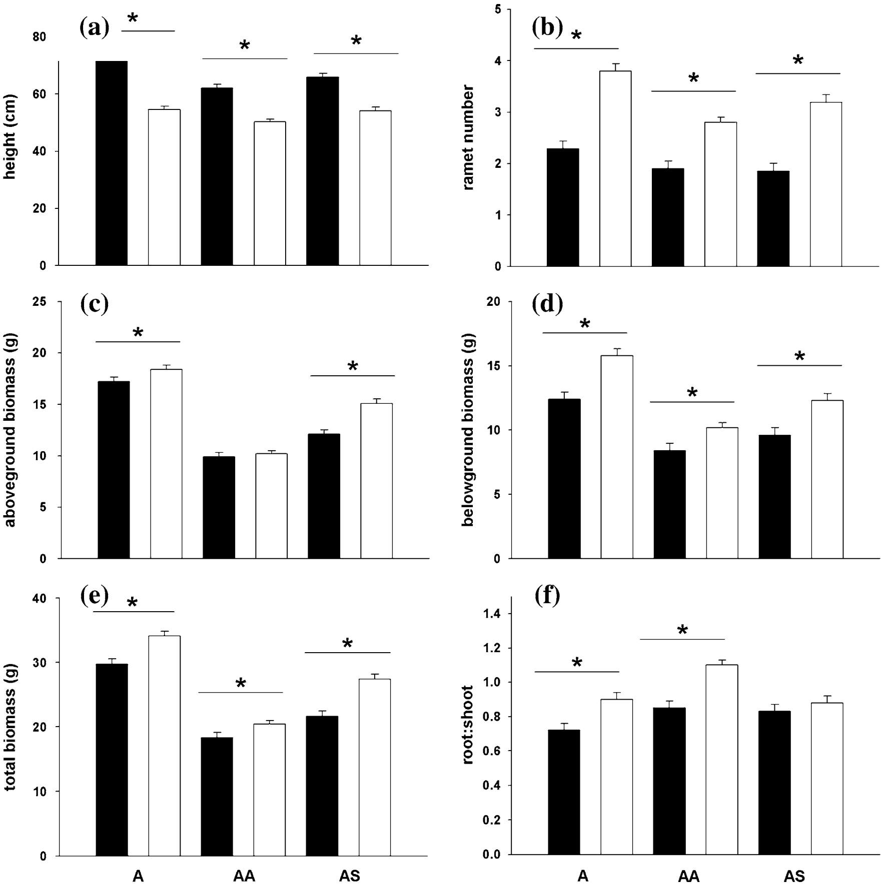

Fig. 1 Height (**a**), number of ramets (**b**), aboveground (**c**), belowground (**d**), and total biomass (**e**), and R/S ratio (**f**) for native (EU—solid) and introduced (NA—open) populations across the competition treatments: *A. vulgaris* grown alone (A), two *A. vulgaris* plants (AA), and *A. vulgaris-Solidago* mixture (AS). For competition treatment comparisons between native and introduced populations, asterisks indicate significant differences at $P < 0.017$ based on pairwise contrasts

Table 3 Relative Cpi and RCI as percentages (±SE) for European (EU) and North American (NA) *A. vulgaris* populations and *Solidago* (S). Pairwise contrasts were made between origins within a treatment comparison. Origins followed by a different letter within a treatment comparison are significantly different at $P < 0.05$

Treatment comparison	Origin	Height	Number of ramets	Aboveground biomass	Belowground biomass	Total biomass	R/S
$\text{Cpi} = \left[\left(P_{\text{single}} - P_{\text{comp}}\right)/P_{\text{single}}\right] \times 100$							
A–AA	EU	11.1 (2.5)a	5.6 (7.7)a	41.8 (2.7)a	31.6 (4.4)a	36.8 (1.5)a	−19.6 (8.7)a
	NA	8.2 (2.7)a	22.4 (7.1)a	41.5 (2.5)a	33.2 (3.9)a	39.6 (1.8)a	−15.9 (8.0)a
A–AS	EU	8.4 (4.9)a	17.1 (8.6)a	30.0 (4.2)a	20.1 (6.1)a	25.2 (4.4)a	−15.0 (7.1)a
	NA	0.6 (5.5)a	16.2 (9.6)a	16.6 (4.6)b	20.5 (6.8)a	20.6 (4.7)a	4.8 (8.0)a
S–AS	EU	24.7 (2.2)a	23.1 (1.5)a	62.1 (1.4)a	67.6 (2.6)a	46.5 (2.3)a	17.3 (6.4)a
	NA	28.1 (2.7)a	26.3 (2.0)a	66.8 (2.8)a	78.2 (2.0)b	38.0 (4.5)b	36.4 (5.3)a
S–SS[A]	S	7.0	50.8	49.3	66.1	59.0	36.5
$\text{RCI} = [(P_{\text{mono}} - P_{\text{mix}})/P_{\text{mono}}] \times 100$							
AA–AS	EU	−7.0 (3.2)a	−2.2 (12.1)a	−24.2 (4.4)a	−20.0 (7.9)a	−20.2 (5.3)a	1.4 (5.6)a
	NA	−8.0 (3.1)a	−12.3 (11.1)b	−44.5 (7.9)b	−21.2 (8.2)a	−32.0 (7.4)a	15.0 (6.0)a
SS–AS	EU	19.0 (2.4)a	11.8 (1.7)a	25.2 (2.7)a	4.6 (7.8)a	−30.4 (5.7)a	−30.2 (10.0)a
	NA	22.7 (2.9)a	15.5 (2.3)a	34.4 (5.4)a	35.8 (5.8)b	−51.1 (10.9)a	−0.1 (8.4)b

[A] No standard error exists for the S–SS comparison plants were, on average, much shorter than native *A. vulgaris* plants, despite producing more aboveground biomass. This is a consequence of individuals from the introduced range investing in a greater number of relatively short ramets with an enhanced belowground root/rhizome network, while native populations invested in fewer, relatively tall ramets. In the absence of competition, introduced *A. vulgaris* individuals produced substantially more belowground and total biomass, more ramets, and had a higher R/S ratio than native populations. In the presence of a competitor, introduced *A. vulgaris* performed better than native populations for most ecological traits measured. Our results partially support the hypothesis of more competitive populations in the introduced range via the evolution of an 'invasive phenotype' (sensu Blossey and Notzold 1995).

We found only five studies examining an invasive phenotype in the published literature that included an inter-specific competition treatment (Blumenthal and Hufbauer 2007; McKenney et al. 2007; Blair and Wolfe 2004; Leger and Rice 2003; Vilà et al. 2003), and two studies that incorporated an intra-specific competition treatment (Bossdorf et al. 2004; Leger and Rice 2003). Vilà et al. (2003) found that aboveground biomass of the North American invader St. John's wort (*Hypericum perforatum* L.) was reduced 90% when grown in inter-specific competition with *Lolium multiflorum* Lam. Another North American invader, *Silene latifolia* Poiret, produced 50% fewer leaves when grown in competition with a grass mixture (*Festuca rubra* L., *Festuca arundinacea* Schreb., *Lolium perenne* L., *Cynondon dactylon* L. (Pers.)) than when grown alone (Blair and Wolfe 2004). Similarly, in Chile, the invasive California poppy (*Eschscholzia californica* Cham.) produced less aboveground biomass and fewer flowers when grown in inter- and intra-specific competition than when grown alone (Leger and Rice 2003). Aboveground biomass and silique production of the invasive biennial herb, garlic mustard (*Alliaria petiolata* (M. Bieb.) Cavara and Grande) were reduced 67 and 99%, respectively, when grown in intra-specific competition, while height was unaffected (Bossdorf et al. 2004). Blumenthal and Hufbauer (2007) found that across 14 species, individuals under no competition outperformed those under low and high competition. Similarly, in our study, *S. canadensis* competition reduced *A. vulgaris* aboveground, belowground, and total biomass, and ramet number compared with *A. vulgaris* grown alone (Fig. 1).

Clearly, including a competition treatment in such biogeographical comparisons is critical to assess the evolution of increased competitive ability. However, only the occurrence of a significant origin (native versus introduced) by competition treatment interaction would indicate that populations from the two continents responded differently to the presence of a competitor. If introduced populations maintain more competitive phenotypes (higher fitness) relative to native populations when a competitor is present, this suggests that introduced and native populations differ in competitive ability (Blair and Wolfe 2004). Of the six studies listed above, only Leger and Rice (2003) and Blumenthal and Hufbauer (2007) reported a significant origin by competition interaction. Introduced *E. californica* populations produced more aboveground biomass and flowers than native populations (Leger and Rice 2003) and Blumenthal and Hufbauer (2007) reported 14 non-native species produced more aboveground biomass than their native conspecifics. Regardless of phenotypic differences, the lack of statistical origin by competitive environment interaction in *A. petiolata*, *S. latifolia*, and *H. perforatum* suggests no shift in competitive ability since the introduction despite phenotypic shifts (Blair and Wolfe 2004; Bossdorf et al. 2004; Vilà et al. 2003). McKenney et al. (2007) found no phenotypic differences between introduced and native populations of the perennial forb *Lepidium draba* whether grown with a strong or weak competitor. In our study, a significant origin by competitive environment interaction was found for height, total number of ramets, aboveground and total biomass, and R/S ratio with introduced *A. vulgaris* outperforming native populations in inter-specific competition with *Solidago*.

A comparison between phenotypes grown alone and with a competitor does not, however, adequately address whether an invasive phenotype has evolved, because we would expect individual plants to be smaller when two plants are competing for the same resources within a limited soil volume relative to a single plant (Tilman 1982). The establishment of a replacement series that includes multiple proportions of each species, or an additive design using a range of densities, would be most appropriate to assess competitive ability (Freckleton and Watkinson 2000; Jolliffe 2000). However, experimental limitations where large numbers of populations from different origins are used often preclude using these elaborate designs. Instead, in addition to an inter-specific competition treatment, we also included an intra-specific (same population) competition treatment to address the question of how neighbor identity affects the introduced and native *A. vulgaris* phenotypes (sensu McKenney et al. 2007). Several studies have demonstrated that neighbor identity can alter phenotypes (e.g., Reader et al. 1994), but we are most interested in the relative effects of neighbor identity. We calculated the RCI to assess neighbor identity effects, with a negative value (AA < AS) indicating that *A. vulgaris* is a superior competitor against *Solidago* than with itself. Additionally, a more positive RCI for *Solidago* (SS-AS) represents greater suppression by an *A. vulgaris* neighbor than a *Solidago* neighbor. Therefore, if these competition indices are greater for introduced than native *A. vulgaris*, we can conclude a shift toward increased competitive ability, and enhanced suppression of a common introduced range competitor, which would support the origin by competitive environment interaction found previously.

The RCI for *A. vulgaris*, with the exception of the R/S ratio, was negative for both native and introduced populations, indicating *A. vulgaris* maintains higher fitness in the presence of *Solidago* than another *A. vulgaris*. As predicted, introduced *A. vulgaris* RCI was greater than native *A. vulgaris* for the competitively important traits of ramet number and aboveground biomass, suggesting introduced populations fair much better against *Solidago* relative to themselves than do native *A. vulgaris* populations. Additionally, *Solidago* belowground biomass was more highly suppressed when paired with an introduced *A. vulgaris* individual than a native *A. vulgaris* individual. Our findings support the conclusion that introduced *A. vulgaris* individuals that invest more heavily in belowground biomass were more competitive than native *A. vulgaris* individuals that invest more heavily in aboveground biomass against a common introduced-range competitor of similar life history.

In addition to a shift in phenotype between geographic ranges, *A. vulgaris* also displays plasticity in nearly all ecological traits measured. In the parlance of Richards et al. (2006), *A. vulgaris* appears to be a Jack-and-master for the traits measured under the conditions imposed. A species exhibiting Jack-and-master plasticity performs best under favorable conditions (i.e., no competition in our study) and maintains lower, yet still high performance under less favorable conditions (i.e., presence of competitor). In our study, *A. vulgaris* always did best with no competition, while performance was lower, but varied little between inter- and intra-specific competitions. Additionally, the introduced populations outperformed native populations for all ecological traits measured (except height), which Richard et al. (2006) predict for fitness plasticity of an invasive species.

Our study period was intentionally short to elucidate competitive mechanisms and hierarchies that manifest early and are maintained (often non-linearly) throughout the life of the population, with species and/or individuals establishing early becoming dominant (Barney et al. 2005; Weiner 1990). Previous studies have demonstrated that *A. vulgaris* populations that establish rapidly early become more abundant in successive years (Barney et al. 2005). Shifts in phenotype and competitive hierarchies in our study occurred in the crucial stages of population establishment of a perennial species—seedling to flowering. Additionally, we were concerned with terminating the experiment before target plants flowered to preclude the creation of novel genotypes and potential escapes of this difficult to control perennial. Results should also be viewed within the context of the treatments imposed. Neighbor identity and density would likely change the magnitude of the ecological traits measured.

To the best of our knowledge, this is the first study to quantify both aboveground and belowground performances under both inter- and intra-specific competitions of an invasive species. Our results suggest that since initial introduction to North America in the early nineteenth century (Barney 2006), *A. vulgaris* has shifted from being largely an aboveground competitor in the native range (i.e., producing relatively few tall ramets) for being a dominant belowground competitor in the introduced range, as highlighted by the production of numerous relatively short ramets with more extensive rhizome networks. This demonstrates a shift in competitive architecture from aboveground to belowground dominance, and provides partial support for the evolution of a more competitive phenotype. Additionally, *A. vulgaris* possesses plasticity for ecological traits to maintain high performance in response to the presence of competitors. We did not assess the predicted decrease in defensive compounds or increased herbivory susceptibility (no variation was observed in what very little herbivory we noted) in introduced populations (Blossey and Notzold 1995). However, the more competitive invasive phenotype documented here may increase the probability of establishment, and ultimately dominance, in native ecosystems comprising species of similar life history.

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